STUDIES FOR STUDENTS.

THE DEVELOPMENT AND GEOLOGICAL RELATIONS OF THE VERTEBRATES.

IV. AVES.

THAT the birds were derived from the reptiles there is little doubt, the structure of the limbs, head, the thoracic and pelvic girdles and the feet all show a close resemblance to that of the same regions in the reptiles. Especially is this true in the more primitive birds. The general characters that are used to distinguish the class *Aves* are the development of the anterior limbs as flying organs and the accompanying atrophy of the digits of the front foot; the fusion of the bones of the skull to form a solid brain case; the fusion of the bones of the pelvis to form a solid mass of bone; the fusion of more or fewer of the dorsal vertebræ and the development of feathers. To these characters there might be added for all recent birds the absence of teeth. In the most primitive bird that we know there is not one of these characters developed in anything like a complete state, except the presence of feathers. In fact, if it were not for the fortunate accident of the preservation of the fossil in the fine grained beds of the Lithographic slates of Solenhofen, so that a cast of the feathers has been preserved, there would be some difficulty in deciding the true nature of the animal. The bones of the head and the pelvis are not coössified; the digits of the anterior limb are developed with functional claws; the vertebræ are distinct and there are many teeth in each jaw.

The Dinosaurs have been regarded as the direct ancestors of the birds, both *Compsognathus* and *Ornithomimus* of the Theropodous division having been considered as the forms from which they were derived, however there is not sufficient proof to

warrant our acceptance of either of these forms. Haeckel in his work on the phylogeny of the vertebrates thinks that the ancestor of the birds must be sought among the most primitive of the Dinosaurs of the Triassic or even earlier, among the *Rhyncocephalia* and the *Proganosauria*. Smith Woodward in his very recent work on Vertebrate Palæontology is content to say, "The earliest known birds exhibit a distinct approach to the *Reptilia* in several characters, but do not afford any indication as to the particular group from which they evolved. The general opinion is, that they are more closely related to certain *Dinosauria* than to any other forms hitherto discovered."

Following the classification adopted by Smith Woodward and in Parker and Haswell's Zoölogy, the class *Aves* may be divided into two subclasses, *Archæornithes* and *Neornithes;* the same groups were called by Haeckel, *Saururae* and *Ornithurae*. The first subclass is characterized by the features mentioned above. There is but one genus known and this is represented by but three specimens, two nearly perfect skeletons and a single impression of a feather.

Archæopteryx from the Lithographic Beds of the Upper Jurassic of Bavaria. Besides the characters mentioned above the animal was distinguished by the possession of a very long bony tail with a pair of feathers growing from each vertebra. The body of the animal was well covered with feathers and the remiges of the wings were well developed. It was about the size of the ordinary crow.

The *Neornithes* are divided into two groups, the *Ratitæ* and the *Carinatæ;* the flightless and the flying birds. The first group is of rather variable limits, some authors including in it all the birds without wings or with poorly developed wings without a keel upon the sternum, and without considering the origin of the condition, whether it is original, persistent from very early forms, or whether it is the result of degeneration from lack of use. Thus Smith Woodward includes among the *Ratitæ* certain forms that are considered by other authors degenerate *Carinatæ*.

The divisions *Ratitæ* and *Carinatæ* are assigned different values by the various writers on the subject, some considering them as orders and the other groups of the birds suborders, while others regard them as divisions of their class and all the other groups as orders. Probably the latter has the greatest following among zoölogists. It will be possible here to consider only those groups that are of importance in geological history.

Æpyornithes: extinct, gigantic birds represented by fossils from the post-Pleistocene of the island of Madagascar. They resembled the living *Apteryx* of New Zealand. *Æpyornis* is the most typical genus. It was of great size, the long bone of the leg, tibio-tarsus, was about two feet and a half long. In general form the members of this and the succeeding order resembled the modern ostriches.

Immanes.—The "Moas" or *Dinornithidæ*, were gigantic forms that existed as late as historical time, they were hunted by the natives of the island of New Zealand, where they were developed. They are not known from formations earlier than the Pleistocene, with the possible exception of a few fragments from what may be the Pliocene. They closely resemble the living *Apteryx*, and are sometimes grouped with it and the Emus and Cassowaries in an order *Megistanes*.

Dinornis is the best known of the genera; the scapular arch was almost entirely atrophied and the sternum was entirely without a keel; the hind legs were very stout and strong; the largest known species stood a little over ten feet high.

Pachyornis was remarkable for the massive nature of the hind limbs; as a whole the animal was smaller than the *Dinornis*.

Most of the existing Ratite birds are known from the superficial deposits of the countries where they are now found; an extinct Emu is known from the eastern part of Australia; remains of Rheas are found in South America and the Ostriches are represented by remains from the Siwalik Hills of India and from the Island of Samos in the Mediterranean.

Carinatæ.—Next to the *Archæopteryx*, probably the most interesting group of birds that is known are the peculiar toothed

forms from the Niobrara Cretaceous of Kansas. These were described by Marsh and called by him the *Odontornithes*, he distinguished two orders, the *Odontolcæ* and the *Odontormæ* (*Icthyornithes*).

Odontolcæ: large, flightless, swimming and diving birds that resemble the modern diving birds, Loons, etc., in many respects, and the Ratite birds in others. The front limbs are almost entirely atrophied, the humerus being represented by a slender stylet of bone; the skull was elongate and the jaws were furnished with many sharp teeth that were set in a common groove for each jaw.

Hesperornis, the most typical genus, was a large form about three feet high. A similar form *Enalornis* is indicated by remains from the Greensand of Cambridge, in England, but the structure of the anterior limbs is as yet unknown.

Odontormæ (*Icthyornithes*): much smaller birds than the former with well developed wings; the jaws were long, as in the preceding genus and were provided with teeth that were set in individual sockets; the vertebræ were peculiar in that the faces, both anterior and posterior, were deeply concave. The bird was much like the modern Tern in external characters.

Icthyornis is the only well-known genus from the Niobrara Cretaceous of Kansas.

The modern birds have many representatives among the fossil forms of the late Tertiary, among the most interesting of these are :

Gastornis, a large flightless bird from the lower Eocene of the western part of Europe. It was peculiar in that the bones of the skull remained separate instead of forming the usual solid brain case.

Apatornis, *Diaphaptoryx*, and *Aphanapteryx* from New Zealand, the Chatham Islands, and Mauritius respectively were gigantic rails that greatly resembled certain of the living rails.

Phororachos was an enormous raptorial bird whose remains are found in the Tertiary of Patagonia.

The Dodo (*Didus*) and the Solitaire from the islands of

Mauritius and Rodriguez were large ground pigeons that had lost, to a great extent, the use of the wings; they were found living by the first travelers that visited the islands, but were speedily exterminated.

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V. MAMMALIA.

The earliest known remains of the mammals are from the Triassic rocks of England and America. Between these earliest of the mammals and their direct reptilian ancestors there is but a very little gap, even in the imperfect record afforded by palæontology. Every step in the transition from the reptilian structure to the mammalian can be traced in the fossil forms, except the final disappearance of a separate bone in the skull, the quadrate, which supports the lower jaw, and the coalescence of the many bones of the lower jaw to form the single mandibular bone of the mammals.

Recalling the structure of the Theriodont and the Gomphodont reptiles of the Permian time we have no need to be surprised at the early appearance of the mammals in time. Speaking of the origin of the mammals, Osborne has said: "Two of the types of the Theromorphs of the Permian and Lower Triassic, namely, the *Theriodontia* and *Gomphodontia*, supply many of the characters which we have expected to find in the ancestry of the Mammals. In fact, they embrace the few osteological characters placed in Haeckel's Promammalia, or Huxley's Hypotheria, as well as the more numerous characters which we have

subsequently put into the mammal archetype. The *Theriodontia* resemble in their dentition and structure the minute *Protodonta* described by Osborne from the Triassic, but differ in the compound character of the jaw bones, as well as in their surpassing size. In tooth structure they are also prototypes of the *Triconodonta* or Marsupials of the Jurassic period. On the other hand, the herbivorous *Gomphodontia*, including *Tritylodon*, are prototypes of the great phylum of Multituberculata, which, in turn, upon extremely slender evidence, however, have been associated with the Monotremata."

So close is the resemblance between the reptiles and the mammals at this point that one of the *Gomphodontia*, the Tritylodon mentioned by Osborne, was originally described from the skull as a mammal by Owen. The Mammalia are generally divided into three subclasses, the *Prototheria*, *Metatheria*, and *Eutheria*.

PROTOTHERIA a small group comprising among the living forms only the peculiar Monotremes, the Duckbill (*Ornithorhynchus*), and the Spiny Anteater (*Echidna*) of Australia. The animals are characterized by the possession of a distinctly reptilian type of shoulder girdle, with distinct interclavicle and coracoid bones; by the presence of a single external opening for the excretory and genital organs and by their oviparous method of reproduction. The Duckbill has an edentulous horny covering to the jaws in the adult stage that has given it its name, but in the very young there are two or more broad flat teeth in each jaw that recall very strongly the teeth of the *Gomphodontia*. There are no fossil remains of these forms known earlier than the Pleistocene. The bones of a large species of the Echidna have been found in deposits of that age in Australia.

The number of forms of the fossil mammals is so great that it will be impossible to discuss many individual genera, as was done with the preceding groups, and in all except especially important cases the descriptions must be limited to the families or even larger divisions.

METATHERIA, animals usually called *Marsupalia;* possessed of

a pouch in which the young are borne by the mother for some time after birth; there are a pair of bones in the abdominal wall that are attached to the anterior end of the pubis on each side and support the pouch; the shoulder girdle is of the usual mammalian type.

Multituberculata, or *Allotheria*, as they are sometimes called, is a group of rather doubtful relations; they have been regarded as belonging to both the *Prototheria* and *Metatheria*, but probably belong with the latter; they are known only from fragments of the skulls and from isolated teeth. The time range of the forms is rather limited, extending from the Upper Jurassic to the Upper Cretaceous. There are three families known: the *Bolodontidæ*, *Plagiaulacidæ*, and the *Polymastodontidæ*.[1]

Bolodontidæ: forms in which the premolars are somewhat molariform and the upper ones have four tubercles. The molars of the upper series have two rows of tubercles. There were strong incisor teeth. *Bolodon*, from the Purbeck layers of Dorsetshire; *Allodon*, from the Upper Jurassic of Wyoming; *Chirox*, from the lowest Eocene, Puerco, of New Mexico.

Plagiaulacidæ: known mostly from the teeth of the lower jaw. The incisors large and rodent-like, the premolars different from the molars, compressed laterally, the posterior one much larger than the rest, and having the side corrugated by deep grooves that extend diagonally in an antero-posterior direction, making the tooth a most efficient grinding organ. The molars low and flat, the lower with two and the upper with, probably, three

[1] The student must recognize that after the mammalian type of life was developed there were no changes in that group of a magnitude comparable with those which produced the various groups of the reptiles. Until comparatively recently the changes considered have been those which centered in the development of the teeth and the limbs, and it was by the study of these changes that the morphology and the classification of the various groups has been worked out. It will thus be necessary to speak in some detail of these regions. For information on this subject the student is referred to the chapter on Kinetogenesis, chap. vi, in PROFESSOR COPE'S last book, Primary Factors of Organic Evolution, published by the Open Court Publishing Company of Chicago, 1896. The book has an especially valuable bibliography of the same subject. PROFESSOR OSBORNE has published in the American Naturalist for December 1897, an illustrated article bearing on the same subject entitled "Tritubercly: A review dedicated to the late Professor Cope.

series of tubercles. *Microlestes*, Upper Trias, Rhaetic, of Wurtemberg and England; *Plagiaulax*, Purbeck of England; *Ctenacodon*, Upper Jura of Wyoming; *Ptilodus*, Puerco Eocene, of New Mexico, under this last name Osborne includes as synonyms most of the names given by Marsh to the forms described by the latter author from the Laramie Cretaceous; *Meniscoessus*, from the Laramie Cretaceous of Wyoming, under this name are grouped as synonyms many of the remaining described forms from the same region. *Neoplagiaulax*, from the lowest Eocene of France; *Abderities*, as well as many imperfectly known forms, from the Eocene, Santa Cruz formation, of Patagonia.

Polymastodontidæ: lower jaw with a very large and strong incisor tooth greatly resembling that of the recent rodents, two large molars with two rows of tubercles and a very small premolar. This form is quite near the rest of the group, but is easily distinguished by the absence of the enlarged premolars and the much larger size of the animal.

Polymastodon, from the Puerco Eocene of New Mexico.

The study of these forms has led to the best knowledge we have of the changing conditions at the end of the Mesozoic time; thus from a comparison of the similar types in the preceding and the succeeding ages we are led to the conclusion that as far as the faunal relations go the Eocene is very much nearer to the Upper Cretaceous than is the Jurassic, and this means, possibly, a slighter change in the conditions, climatic and otherwise. Osborne says: "The Laramie mammals are surprisingly near to those of the Puerco, and in some cases almost identical with them; in other cases they are of a somewhat older type, ... the greatest gap to be filled by future discovery is between this Laramie fauna and the Jurassic. For this Laramie fauna is separated from the Puerco about as widely as the Puerco is from the Wasatch, but no more widely; whereas it is separated by a profound gap from the Jurassic fauna."

The *Marsupalia*, *Metatheria* proper, is divided into two groups, the *Polyprotodonta* and the *Diprotodonta*, according to the presence of two or more than two incisor teeth in the jaws.

Polyprotodonta: carnivorous or insectivorous forms of small size with a large number, 4–5, of incisor teeth and many molar and premolar teeth, 8–12 in opposition to 6–7 possessed by recent forms. The premolars are simpler than the molars.

The suborder is divided by Osborne into three groups, *Protodonta*, *Triconodonta*, and *Trituberculata*. The first, the *Protodonta*, is distinguished by having the premolars simple and conical in shape and the molars with a middle part slightly elevated above a posterior and an anterior accessory cone. The molar teeth are single-rooted, but there is a deep groove on each side that indicates the coming division of the root into two parts. The group is represented by two specimens only. These are from the Triassic rocks of North Carolina and consist of the lower jaws only. *Dromotherium* and *Microconodon.*

Triconodonta: forms very similar to the last, but with a smaller number of molar teeth. The middle cone of the molars is better developed and the accessory cones are separated farther from the main one and have a much greater part in the function of mastication. The roots of the teeth are entirely separated. The forms are almost entirely from the Jurassic layers of England, and Wyoming. Typical genera are:

Amphilestes, Oolite from near Oxford, England.

Phascalotherium, Oolite from near Oxford, England.

Tinodon, Upper Jurassic of Wyoming.

Priacodon, Upper Jurassic of Wyoming.

Dicrocynodon, Upper Jurassic of Wyoming.

Trituberculata: small forms with many molar teeth, the crowns of which are supplied with three tubercles arranged in the form of a triangle with apex of the triangle pointing inwards in the upper teeth and outwards in the lower; the importance of these forms is best realized when we remember that this tritubercular arrangement of the tubercles of the teeth is the primitive type from which all the remaining types of mammalian dentition have been derived. The *Amphitheridæ* and the *Amblotheridæ* are the two most primitive families of the suborder.

Amphitherium, from the Oolite of England, near Oxford.

Amblotherium, from the Purbeck of England.

Dryolestes, from the Upper Jurassic of Wyoming.

The *Myrmecobidæ*, *Peramelidæ*, *Dasyuridæ*, and *Didelphyidæ* are all families containing living forms, the last two have members from rocks as old as the earliest Eocene. It is of interest to note that while the family *Didelphyidæ*, the opossum, is at present confined to the North and South American continents it formerly ranged over the whole of Europe and England.

Diprotodonta.— This suborder is distinguished by the presence of only two incisor teeth in the upper jaw and one in the lower. The premolars are like the molars, or may be developed as long cutting organs, as in the *Allotheria*. There are several families, but only two are of interest to us here, as they are the only ones that contain fossil forms. The suborder, living forms as well as extinct, is entirely confined to the Australian region.

Thylacoleo is the single representative of the *Thylacoleonidae ;* it was a large form about the size of the lion, with strong incisors and one of the premolars in each jaw greatly elongated in the antero-posterior direction, and compressed from side to side so as to form a long cutting edge; the rest of the dentition is quite weak. The posterior part of the head is very wide, but it narrowed rapidly as it approaches the anterior end.

Diprotodon and *Nototherium* are the representatives of the *Diprotodontidae*. The skull of the first was nearly three feet long, the incisor teeth were developed as gnawing teeth, with enamel on the outer side only and set in deep alveoli. The posterior teeth lacked the cutting edges of *Thylacoleo*, and were adapted to grinding up vegetable material. The whole form had the bulk of the rhinoceros; the structure of the feet is unknown. *Nototherium* was very similar to this form, but was considerably smaller.

EUTHERIA: Animals in which there is no marsupium; the embryo is nourished by the development of a placenta that attaches it to the mother. This includes all the remaining forms of the mammals. Palæontologists recognize ten orders of the

Eutheria: the *Cetacea*, *Sirenia*, *Ungulata*, *Tillodontia* (*?*) *Rodentia*, *Carnivora*, *Insectivora*, *Chiroptera*, *Edentata and Primates.*

Edentata.—These are the lowest of the Eutheria in the scale of development. The group is characterized by the imperfect development of the dentition; the teeth are few in number, and the enamel is lacking from the surface in the more recent forms. That they are degenerate forms is shown by the fact that the earlier order had perfectly formed teeth; many of the steps in process of degeneration have been traced. Three suborders are recognized: *Nomarthra*, *Xenarthra*, and *Ganodonta*. The first of these is of little importance from a palæontological standpoint; it is composed of forms confined to the tropical parts of Asia and Africa. It is separated from the *Xenarthra* by characters of the vertebræ.

The *Xenarthra* is divided into five suborders, the *Tardigrada*, *Dasypoda*, *Gravigrada*, *Glyptodontia*, and *Ganodonta*. The first two are confined to the recent and the later Tertiary of South and Central America.

Gravigrada.—These forms, now extinct, were of gigantic size; the body was large and clumsy with a powerful tail that, perhaps, aided the animal in assuming the upright position; in the later forms, perhaps more than in the earlier, the animals walked with the side of the foot presented to the ground; the teeth were few and confined to the posterior part of the jaws; they were without any enamel upon the surface. The animals were in fact large ground sloths; they probably obtained their nourishment by uprooting trees and shrubs and feeding upon the leaves and smaller branches.

Megatherium was the largest of the forms, reaching a length of 18 to 20 feet, and a height of about 8 feet. The teeth placed close together at the posterior part of the jaw, exhibit cross ridges from the presence of slightly harder dentine. The animal is known from all parts of South America, and as far north as Georgia, South Carolina, and Texas.

Megalonyx.—This form is the representative of a separate family from the preceding; the most anterior of the molar teeth

stands far in front of the remainder, and has the appearance of a canine. The genus appears to be confined to the latest deposits of the Tertiary in the United States, and is found in the cave deposits of the southern states. The animal reached the size of an ox.

Mylodon, another form is distinguished from the others by the appearance of slight irregularity in the form of the teeth; instead of straight peg-like form, they are triangular, and the teeth of the lower jaws are somewhat figure eight shaped in outline. This genus was fully as large as the *Megatherium* and had even a greater geographical range, species being known from the pampas of the Argentine Republic, and from the caves of Oregon.

A very large number of forms have been described from the deposits of Patagonia and the Argentine Republic, and a smaller number from other parts of the southern continent, many being found on the west coast, to reach which place they must have either crossed the Andes, or emigrated down the west coast from far up in the United States. The geological range seems to have been from the upper Eocene or the Oligocene to the latest Pliocene.

Glyptodonta.— These were animals in which the body was covered by a strong carapace of bone that was made up of many small ossicles of different shapes, joining each other by suture. The armor was confined entirely to the dorsal surface, there being no plastron or ventral plate as in the turtles. The tail was large and covered with the same armor as the back. The skull was very short and high with a lower jaw of great vertical thickness. The teeth were elongated in the anterior-posterior direction, and the sides of the teeth were marked by deep vertical grooves that nearly divided the teeth into three parts. The vertebræ of the dorsal region were all united into a long tube, and the lumbar vertebræ were anchylosed with the sacrum, thus practically destroying any mobility of the spine. The feet were provided with broad, almost hoof-like claws. The animals sometimes reached a very large size. The whole suborder is extinct.

Glyptodon: a very large form that ranged from the southern part of South America as far north as Texas and Florida. The animal was about six feet long, and reached a height of three feet at the most elevated portion of the carapace. The dermal plates are sculptured in the form of a rosette. The tail is covered with a series of bony rings that are attached to the processes of the vertebræ within.

Panocthus: a large form that is confined to southern part of South America; very similar to the *Glyptodon*. The carapace was made up of four and five-sided pieces with a tuberculated surface instead of the rosette arrangement. The anterior part of the tail was protected by 6–7 large bony rings, but the posterior part was enclosed in a solid tube of bone that was slightly flattened; the surface of this tube was covered with small plates that in places gave room to larger ones that seem to have been the bases of some sort of protuberance, horny or bony. The form reached about the size of a rhinoceros.

A large number of these forms have been described from the late Tertiary deposits of Patagonia, and the Argentine Republic. The majority of them come from the Miocene and the Pliocene, though a considerable number are from the earliest, the Santa Cruz Tertiary.

Ganodonta.[1]—This group was founded in 1896 by Wortman, and considered by him as a suborder of the Edentata. The group is made up of a part of the order *Tillodontia*, which was originally considered as the ancestral form of the rodents. Not until the teeth of one of these forms was found in connection with the fore limb was it determined that they were Edentate in character. The fore limbs are similar in every respect to those of the *Tardigrada*, but the teeth are different in that they are not devoid of the enamel covering and in the presence of the anterior teeth, the incisors, and the canines. These forms occur in the earliest Eocene Puerco beds of New Mexico, and are undoubtedly the earliest forms of the Edentates. They are of

[1]Science, December 11, 1896, p. 865., Bull. Am. Mus. Nat. Hist., Vol. IX, p. 59. (Contains a full description of the Ganodonta and its geological relationship.)

extreme interest as indicating the origin of the group which has been for long one of the greatest problems of the palæontologist. Other than the interest attaching to the origin of the group is that of the geological possibility of the forms getting into the southern continent in the early Tertiary time. These forms undoubtedly originated in the United States. As there is no trace of them in the basal Eocene of South America. and they appear in great numbers and highly developed in the Middle Eocene, it seems certain that they must have emigrated from the northern land. There is little possibility that they could have taken the northern route and gained the land of Asia by the northern connection, and then worked into South America by the Antarctic continent; this is further borne out by the fact that there are no known remains of the group from the Old World beyond the incompletely identified specimen of one genus. It seems probable that there must have been a temporary connection between the two continents in the earliest or the Middle Eocene. That the forms found the conditions of life exceptionally favorable in the southern continent is evidenced by the extraordinary development both of species and of individuals.

Cetacea.—This order bears very much the same relation to the land mammals that the Plesiosaurs and the Icthyosaurs bore to the early land reptiles. The limbs have degenerated and become adapted as swimming organs, the bones of the proximal portions becoming shorter and losing their distinctive character, while the phalanges become much more numerous and there may even be added digits. In most of these forms also the hind limb is lost; the teeth become simpler and disappear in some forms; the whole body takes on the fish-like form that seems to be requisite for the aquatic life; the hair disappears and is represented by only a few scattering bristles. These remarks are equally applicable to the succeeding group, the *Sirenia*.

The *Cetacea* are generally divided into three groups, the *Archaeoceti*, the *Odontoceti*, and the *Mysticoceti*. The last two groups, the recent dolphins and the whales are represented in the fossil state by specimens from the Eocene, showing all the

characters of the recent forms. The first group, the *Archaeoceti*, is represented by a form that is known from all parts of the world, *Zeuglodon;* it has an elongate skull like the alligator, but still possesses the dentition of the land animals, in that it is differentiated into premolars and molars; the position of the nostrils and the extent of the nasal bones are also typical of the land forms, but the limbs are those of a water animal. As the form is the earliest known, it is regarded as the nearest to the primitive ancestor of the *Cetacea*. The carnivorous dentition has led to the conclusion that it, and consequently all of the order was derived from a carnivorous mammal. The high degree of development of the order at its earliest appearance, indicates that these animals must have begun their specialization some time in the Cretaceous before we know of any mammals that could have produced them.

The *Sirenia* have a like history to the foregoing group. They are, without doubt, the descendants of land-living forms, but are derived from ungulates, probably from the primitive *Condylarthra*, instead of from carnivorous forms. The earliest remains are from the Eocene rocks, and show that the animal was at that time still in possession of a pair of rudimentary hind limbs. Specimens are known from most of the countries of the earth, and from all deposits from the earliest Eocene up. *Rhytinia*, Steller's Sea-cow, became extinct as late as the middle of the eighteenth century. It was found in great abundance on the shores of Alaska and the neighboring islands by the early explorers, and was slaughtered for food by the whalers.

Ungulata.—This is one of the largest groups of the mammals, including all of the herbivorous forms with the exception of the rodents. They are all land-living forms, with the limbs modified as organs of locomotion and the terminal phalanges armed with broad, flat, horny coverings or hoofs. The dentition is adapted to a vegetable diet or to an omnivorous one, as in the pig. The dentition is diphydont, *i. e.*, there is a milk set that is later replaced by a permanent one.

There are generally recognized eight suborders of this order:

Condylarthra.
Perissodactyla.
Artiodactyla.
Amblypoda.
Proboscidea.
Toxodontia.
Typotheria.
Hyracoidea.

The *Condylarthra* are forms with five functional digits on each foot; plantigrade in the habit of walking, and with small hoofs on each digit. The astragulus has a long neck, and the distal articular face, for the navicular, is rounded. The teeth are multitubercular and complete in number in each jaw. It was in these regions that the changes took place that have made it possible to trace out the lines of development of the ungulates, and, as Cope thought, the lines of the *Carnivora* and the *Primates* as well.

There are several families of the suborder, but it will be as well, probably, to take one of the forms from one of the families and describe it as typical of the whole group.

Phenacodus is the best known of the suborder. By great good fortune the nearly perfect skeletons of two individuals are known. The whole animal was about the size of a mastiff dog. The first and fifth toes on both the fore and the hind feet are shorter than the others, and show already the tendency to a reduction in number that is the dominant line of evolution in the foot structure of the ungulates. Another thing, the bones of the two rows of the carpus and the tarsus are arranged one above the other, instead of being alternate in position, *i. e.*, one of the upper row being opposite the space between two of the lower row. The latter arrangement is readily seen to be by far the strongest, and the development of the ungulates is marked by the gradual acquisition of this alternate arrangement of the bones in place of the serial arrangement of the *Condylarthra.* There was a long tail; the skull was low and flat, with large

orbits that are open behind; the multitubercular teeth indicate that the animal was omnivorous in its diet; the brain was small and smooth, devoid of deep convolutions such as exist in most of the mammalian brains.

Periptychus was a very similar form from the same horizon as Phenacodus.

Pleuraspidotherium and *Orthaspidotherium* are forms from the lowest Eocene, Cernays, of France; they are similar in the essential features to the American *Condylarthra*, and show that the group was widespread in its geographical range, as might be expected from its generalized characters.

Starting from the *Condylarthra*, with its generalized dentition and five-toed feet, there were developed two lines of the *Ungulata*, which include all of the living and extinct forms. In one line the weight of the body is borne on the three middle digits of the feet, or, in the more advanced forms, on the middle one of all the digits. These forms were called by Owen, in 1849, the *Perissodactyla*. They are generally referred to as the "odd-toed" animals, with the idea that there is always an uneven number of toes on the feet, but this is erroneous, as some members of the group have four toes on the feet; the essential thing is that only three of them take any part in supporting the body, the other being a rudiment from the original pentadactyl arrangement. The next group of the *Ungulata* is the *Artiodactyla*, the forms with an even number of toes supporting the body. There are, of course, many points in the structure of the two groups that are correlated with the development of the toes; thus, in the first group there are never any horns developed on the parietal bones, and the horns are never paired, but there are horns developed on the median line on the nasal bones, as in the rhinoceros. There is no living form of the *Perissodactyla* that ruminates; there is a characteristic number of dorsal vertebræ for each group; the astragalus of the two groups has a very different form, and there is always a third trochanter on the femur of the odd-toed forms.

Osborne, in Part I of his memoir on the Extinct Rhinoce-

roses, has given perhaps the best summary of the position of these forms. He says: "The Perissodactyla may be primarily divided by the fundamental pattern of their upper grinding teeth into four superfamilies, as follows:

1. TITANOTHEROIDAE: including the single family (1) *Titanotheridæ.*

2. HIPPOIDEA: including the two families (2) *Equidæ* and (3) *Paleotheridæ.*

3. TAPIROIDEA: including the two families (4) *Tapiridæ* and (5) *Lophiodontidæ.*

4. RHINOCEROTOIDEA: including the three families (6) *Hyracodontidæ*, (7) *Amynodontidæ*, and (8) *Rhinocerotidæ.*

To these should be added:

5. CHALICOTHEROIDEA, an aberrant superfamily, with molar teeth related to the Titanothere pattern, and perissodactyl feet provided secondarily with claws.

The eight families, in the order named, may be imagined as the contemporary branches of the four superfamilies, these in turn having branches from a still unknown Perissodactyl stem form — probably a Cretaceous member of the Condylarthra.

These eight families, familiarly known as the Titanotheres, Horses, Paleotheres, Tapirs, Lophiodonts, Hyracodonts, Amynodonts, and Rhinoceroses, when regarded as a series, present upon the one side close resemblances, or perhaps affinities, to the Artiodactyla, and an extreme departure from the Artiodactyla on the other. Thus the Titanothers exhibit many resemblances to the Artiodactyls, while the Rhinoceroses exhibit none at all, and are in many respects the most typical Perissodactyls.

Superfamily RHINOCEROTOIDEA, or Rhinocerotine group. The three distinct families included in this division may be popularly known as the Cursorial or Upland Rhinoceroses, the Aquatic Rhinoceroses, and the True or Lowland Rhinoceroses. They are briefly distinguished as follows:

Hyracodontidæ: cursorial rhinoceroses; *Hyrachyus* and *Hyracodon;* manus functionally tridactyl; upper and lower incisors and canines persistent and uniformly developed.

Amynodontidæ: Aquatic Rhinoceroses; *Amynodon* and *Cadurcotherium;* manus functionally tetradactyl; incisors atrophied; upper and lower canines greatly enlarged.

Rhinocerotidae: True Rhinoceroses; *Aceratherium* and *Rhinoceros;* manus functionally tridactyl; upper canines atrophied; median upper incisors and lower canines opposed and irregularly developed.

Our knowledge of the three divisions of this superfamily extends back only to the Middle Eocene of America and Europe, namely, to the Bridger and the somewhat older Egerkingen Beds of Switzerland. No Rhinoceroses of any kind have as yet been found contemporary with the primitive Horses and Tapirs of the Wasatch of America or the Suessonian of France, but they will undoubtedly be discovered in these or older rocks either in America or Europe, with characteristics as sharply defined as those of the other perissodactyl families.

Certainly before the Middle Eocene of North America, the Rhinocerotoidea had here or in some unknown region specialized and diverged into the three above-mentioned families, which some authors place in the single family Rhinocerotidæ. While it is quite possible that in the Wasatch or Suessonian period this group consisted of a single family, in the Bridger we certainly find two distinct families, the Hyracodontidæ and Amynodontidæ, and in the White River these coexist with the Aceratheriinæ, or ancestral true Rhinoceroses. The members of each family were evidently as widely different in their external form as in their dental and skeletal structure. . . . .

There is no doubt, therefore, that as a matter of taxonomic clearness as well as of phylogenetic fact it is best to consider these three families as entirely separate and undergoing a parallel development, probably in Europe as well as in America.

Specialization in habits.—The wide separation of these three families will be fully apparent after we have examined their chief primitive, parallel, and divergent features. Parallelism is mainly confined to the evolution of the molar teeth, for in every feature of the incisor teeth, the skull, the vertebræ, and the limbs, these

families specialized and diverged rapidly. The rhinocerotine differentiation in the broad sense of the term, imitated that of the Perissodactyla as a whole in its general functional radiation. They ran either into upland cursorial types, which competed with the Horses and the Ruminants, or into the lowland marsh or river dwellers, which competed with the Tapirs and the Titanotheres.

Among the former were the smaller, more agile, light-chested types of Hyracodonts, simultating the Miocene Horses in skeletal structure and in the development of true hoofs. Among the latter were the short, heavy types of Amynodonts, with broad, spreading, padded feet; they probably acquired, like the Tapirs, a long, prehensile upper lip, or, possibly, a true proboscis was developed, in correlation with the rather abbreviated nasals. The elevated and prominent position of the orbit would bring the eye near the surface in swimming. This feature, with the long, curved tusks, undoubtedly used in uprooting, suggests the resemblance between the habits of these animals and those of the Hippopotami. The early Aceratheres were light-limbed rather swift-footed animals, intermediate in proportions between the Hyracodonts and the Amynodonts, but far less graceful and rapid than the former, yet the destiny of this family was also to finally produce both the very slow, heavy-bodied forms, such as *Aceratherium* (*Aphelops*) *fossiger*, of the Loup Fork and the stilted, long-limbed *Aceratherium malacorhinum* of the same period.

Neither the Hyracodonts nor the Amynodonts developed horns, and all the early true Rhinoceroses had weak, hornless, nasals so that they probably appeared externally more like enlarged modern Tapirs than the well-armed animals we are now familiar with.

They did not interfere with each other because each enjoyed a different local habitat, while occupying the general geographical regions. The Hyracodonts dwelt in the drier grassy plains. The Amynodonts frequented the river and lake borders. Up to the time of the extinction of these two related families, the true

Rhinoceroses maintained a somewhat uniform structure, both in Europe and America, differing, so far as we know, in size rather than in proportions. Their dentition and their feeding habits were probably similar to those of the *R. bicornis* of Africa and the *R. sondaicus* and *R. sumatrensis* of Asia, namely, upon leaves, shrubs, and softer herbage. After the extinction of the rival families, however, there was naturally a tendency on the part of the true Rhinoceroses to enter the peculiar local habitats previously occupied by the Hyracodonts and the Amynodonts, and they accordingly diverged into upland and lowland, short and long-limbed, brachydont and hypsodont types.

Geological and geographical distribution.—(1) The Hyracodontidæ, including *Hyrachyus*, *Triplopus*, and *Hyracodon*, are very abundant, displaying a great range of size in the Middle Eocene and Oligocene of North America, and are possibly represented in the Eocene of Europe by species which have been mistakenly referred by Rutimeyer and others to *Lophiodon*. (2) The Amynodontidæ are known from the Upper Eocene or Washakie and Uinta Beds of North America, and are also possibly represented by species referred to *Lophiodon* in the Eocene of Europe, although it is difficult to determine this from the teeth alone; the latest American type is *Metamynodon* of the Oligocene, but *Cadurcotherium* represents a later and probably final stage of development in the Oligocene and Lower Miocene of France. (3) The Rhinocerotidæ are first doubtfully known in the Upper Eocene of Europe, then suddenly appear in abundance in the Lower Oligocene. They are grouped in four subfamilies. (1) Aceratheriinæ of Europe and America. These hornless types ranged through all the Miocene of North America, and then apparently became extinct upon this continent, but in Europe they extended into the Pliocene, and in Asia into the Middle Pliocene. (2) The Diceratheriinæ, or pair-horned types, have been found only in the Lower and Middle Miocene of North America and Europe. (3) The earliest Rhinocerotinæ, or Rhinoceroses possessing median horns, branched off from the Aceratheres in the Middle Miocene of Europe; they divided into three sub-

series which are scattered widely over Europe, Asia, and Africa, and displayed a remarkable specialization. (4). The most aberrant family is the Elasmotheriinæ, thus far found only in the Pleistocene of Siberia."

DISTRIBUTION TABLE, AMERICAN HORIZONS.

	Lower Eocene *Wasatch*	Middle Eocene *Bridger*	Upper Eocene *Uinta*	Oligocene *White River*	Lower Miocene *John Day*	Upper Miocene *Loup Fork*
I. HYRACODONTIDÆ.						
Hyrachyinæ						
Hyrachyus	.....	×				
Colonoceors	.....	×				
Triplopodinæ.						
Triplopus	.....	.....	×			
Hyracodontinæ						
Hyracodon	.....	.....	.....	×		
II. AMYNODONTIDÆ						
Amynodon	.....	×				
Metamynodon	.....	.....	.....	×		
Cadurcotherium [1]						
III. RHINOCEROTIDÆ						
Aceratheriinæ	.....	.....	.....	×	×	×
Diceratheriinæ	.....	.....	.....	.....	×	
Rhinocerotinæ.						

The superfamily TITANOTHEROIDÆ, with the single family *Titanotheridæ* is generally divided into two subfamilies, the *Paleosyopinæ* and the *Titanotherinæ*. The group seems to have developed in the later Eocene time, and to have reached its greatest development in the Miocene near the middle of which time it disappeared. Starting with forms about the size of the Tapirs of modern time the animals gradually increased in size until at the time of their extinction they had reached elephantine proportions. In general appearance they must have been similar to the Tapirs, with a broad, heavy body, stout limbs and a long upper lip. The brain cavity was small, and the brain was probably devoid of deep convolutions. The group reached by far its greatest development in North America, but a few forms have been discovered in the Upper Eocene and the Lower Mio-

[1] Phosphorites of Quercy.

cene beds of Europe. The two subfamilies differed chiefly in the larger size and the more complex dentition and foot structure of the *Titanotherinæ*.

Paleosyops is the most characteristic member of the first subfamily. It is found in the Lower and Middle Eocene of North America (Wind River and Bridger). The dentition was complete, that is, the incisors and premolars were all present; the premolars were simpler than the molars; the skull was without horns and without the concave outline of the upper surface that is so apparent among the Titanotheres. One species was about six feet long and three feet high.

Diplacodon from the Upper Eocene of the United States, Uinta, is of great interest in that it is in many characters related to the Rhinoceroses, and at the same time stands as an almost perfect connecting link between *Paleosyops* of the Lower Eocene and the Titanothers of the Miocene.

Titanotherium was a large form confined to the Lower Miocene and reaching its greatest development in the United States; a few specimens have been found in Europe. Despite the rather short time in which the animal lived upon the earth it developed an astonishing degree of variability, with the result that it has probably received as many different names as any form known. Thirteen genera and thirty-one species have been described from what Osborne, after a careful study of the cranial characters, regards as "one or possibly two genera, and about fourteen definable species." The Titanotheres are characterized by the development of a pair of horns on the anterior portion of the snout; the gradual loss or the tendency to the loss of the incisor teeth; the complex dentition, in which the premolars are as complex as the molars and the increased size. The largest species reached a length of between twelve and fifteen feet and a height of about seven feet. Remains are known from a large number of regions in the United States and Canada, showing that the animal roved over a wide territory.

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